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中国真藓属孢子形态的研究*

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A STUDY ON THE SPORE MORPHOLOGY OF *BRYUM* HEDW. IN CHINA

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Abstract Spore morphology of thirteen species of the genus *Bryum* Hedw. were observed by LM and SEM. The results show that the ornamentation of spore exine could be divided into three types: Type Ⅰ, blunt at the top of baculate processes, to which four species belong: *Bryum argenteum*, *B. lonchocaulon*, *B. uliginosum* and *B. arcticum*. Type Ⅱ, sharp or with small processes at the top of baculate processes, represented by seven species: *B. pallescens*, *B. caespiticium*, *B. pallens*, *B. pseudotriquetrum*, *B. paradoxum*, *B. alpinum* and *B. thomsoii*. Type Ⅲ, expanded into hemispherical-shaped at the top of baculate processes, represented by two species: *B. coronatum* and *B. sauteri*. The *Bryum* species may also be divided into three groups according to the variation of spore diameter. Group Ⅰ, with spore diameter under 10 μm, including one species, *B. uliginosum*. Group Ⅱ, with spore diameter 11～20 μm, including seven species: *B. argenteum*, *B. alpinum*, *B. coronatum*, *B. pallens*, *B. paradoxum*, *B. sauteri*, *B. thomsonii*. Group Ⅲ, spore diameter 21～30 μm, with five species: *B. pallescens*, *B. caespiticium*, *B. pseudotriquetrum*, *B. lonchocaulon*, *B. arcticum*. There are resemblances of spore morphology and exine ornamentation among the thirteen species. In the view of palynology, the genus *Bryum* is a natural taxon which is more advanced than the genus *Pohlia* Hedw. But spores of thirteen species are different at some characters such as diameter, shape of proximal leptoma, etc., which indicates the genetic differentiation in the genus *Bryum*.

Key words *Bryum*; Spore morphology

摘要 通过光学显微镜和扫描电子显微镜观察了中国真藓属 *Bryum* Hedw. 13 种孢子的形态特征。根据外壁纹饰可分为:类型Ⅰ,棒状突起顶端圆钝;类型Ⅱ,棒状突起顶端尖或具微突起;类型Ⅲ,棒状突起顶端膨大成半球形。根据孢子直径的大小,可分 3 个类群。以上显示了物种间的遗传分化及其相似性,证明真藓属确为一个自然分类群,真藓属孢子的形态比丝瓜藓属 *Pohlia* Hedw. 进化。这给苔藓的孢子形态研究及分类和系统演化的研究提供了新的资料。

关键词 真藓属;孢子形态

真藓属 *Bryum* Hedw. 分布于世界各地,常在山地土坡及岩面着生,偶生于树干、树

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枝上。该属分种相当困难，仅有配子体较难鉴定到种，大部分种类则依据孢子体的特征划分。早在19世纪初，Brotherus (1924)将本属分为2亚属22个组。他认为 Subgen. *Ptychostomum* 的蒴齿内面的横格间具斜隔，而 Subgen. *Bryotypus* 则无斜隔。有人认为此特点在其发育过程中可能有较多的变异，不宜作为分亚属的依据，分组同样缺乏稳定的性状。Nyholm (1958)将真藓属分为4个组。主要依据叶片的颜色、叶缘细胞及蒴齿齿毛形态等。按孢子直径划分类群较接近于此分组规律，显示出两者的相关性。1982年，关根雄次综合了日本学者 Ochi (1959)等人对日本真藓科 Bryaceae 的看法，将真藓属分成 Sect. Ptychostomum, Sect. Leucodontium 和 Sect. Eubryum 3个组。在 Sect. Ptychostomum 中，孢蒴内齿层发育不完全，齿毛不发达或退化，蒴口小形。在后两组中，孢蒴内齿层完全，齿毛发达，蒴口较大。Sect. Leucodontium 中，叶片中肋仅至叶片中上部或近尖部消失。而 Sect. Eubryum 中的叶片中肋达叶尖或突出。笔者对中国真藓属13个种的孢子进行光学显微镜(LM)和扫描电镜(SEM)观察，并对其形态特征作较详细的描述，以期为探讨种间亲缘关系提供新资料。

1 材料和方法

研究材料分别采自河北、四川、云南和西藏。光学显微镜观察用材料，经过 G. Erdman 醋酸酐分解法处理(中国科学院北京植物研究所古植物研究室孢粉组，1976)。扫描电镜观察用材料，将风干后的成熟孢子散在透明胶纸上，贴于金属台面，用离子溅射仪喷金镀膜，在扫描电镜 (HITACHI S-800)下观察、照像。每种孢子取20粒测量其直径，求其平均值和最小到最大的变化幅度。凭证标本见表1，凭证标本存于中国科学院植物研究所标本馆和首都师范大学生物系植物标本室。

2 观察结果

真藓属植物，孢子母细胞经减数分裂形成四分体，分离后逐渐发育成球形或近球形的单细胞孢子。孢子多为黄褐色或黄绿色，均具萌发孔(Aperture)，即近极薄壁区。物种间孢子直径差异较大，最小的为9.8 μm，最大的达28.2 μm。在光镜下观察，*Bryum coronatum* 等8个种的孢子外壁显示近于平滑，*B. lonchocaulon* 等5个种的孢子外壁具细疣。然而，扫描电镜观察证实，13个种的孢子的外壁均具棒状突起，但棒状突起的高度以及顶部的细微结构有差异。

各种孢子的特征见表1。

3 讨 论

据观察，真藓属孢子按其外壁纹饰可分为3种类型，按其直径大小可分为3个类群。

3.1 按外壁纹饰划分类型

Ⅰ. 棒状突起顶端圆钝。其种类有：*Bryum argenteum*；*B. lonchocaulon*；*B. uliginosum*；*B. arcticum*。

Ⅱ. 棒状突起顶端尖或有微突起。其种类有：*B. pallescens*；*B. caespiticium*；*B. pallens*；*B. pseudotriquetrum*；*B. paradoxum*；*B. alpinum*；*B. thomsoii*。

表1 真藓属13种孢子的形态特征

Table 1 The spore morphological characters of the genus *Bryum* Hedw.

种 Species	孢子直径 Spore diameter(μm)	萌发孔(SEM) Aperture	外壁纹饰(SEM) Exine ornamentation	凭证标本 Voucher
真藓 *Bryum argenteum* Hedw.	(10.9~) 13.2 (~14.1)	具近似四角形薄壁区(plate Ⅰ:1) forming a quadrangular leptoma	短棒状,着生不规则,常有几个棒状突起侧面相连,呈蠕虫状(plate Ⅲ:4) shortly baculate, arranged irregularly, some processes connected into worm-shaped	Hebei, Mt. Wuling (河北,雾灵山) Du Gui-sen, W9472
刺叶真藓 *B. lonchocaulon* C. Muell.	(25.0~) 27.9 (~31.3)	具多角形薄壁区(plate Ⅲ:7) forming a polygonal leptoma	小棒状或瘤状,着生相对较稀疏(plate Ⅰ:9) finely baculate or tuberculate, arranged rather sparsely	Hebei, Mt. Wuling (河北,雾灵山) Du Gui-sen, W9356
垂蒴真藓 *B. uliginosum* (Brid.) B. S. G.	(7.8~) 9.8 (~10.9)	具三角形薄壁区(plate Ⅰ:6) forming a triangular leptoma	小棒状或瘤状(plate Ⅲ:6) finely baculate or tuberculate	Hebei, Mt. Wuling (河北,雾灵山) Du Gui-sen, W9318
极地真藓 *B. arcticum* (R. Brown) B.S.G.	(25.0~) 28.2 (~31.1)	具四角形薄壁区(plate Ⅲ:3) forming a quadrangular leptoma	棒状,着生相对较稀疏(plate Ⅱ:8) baculate, arranged rather sparsely	Hebei, Mt. Wuling (河北,雾灵山) Du Gui-sen, W9525
黄色真藓 *B. pallescens* Schleich. ex Schwaegr.	(20.3~) 21.8 (~25.0)	具三角形薄壁区(plate Ⅰ:2) forming a triangular leptoma	棒状,顶端有少数微小刺状突起(plate Ⅰ:4) bacullate, with small spinulate processes on the top	Hebei, Mt. Wuling (河北,雾灵山) Du Gui-sen, W9237
高山真藓 *B. alpinum* Huds. ex With.	(10.9~) 12.9 (~15.6)	具多角形薄壁区(plate Ⅲ:1) forming a polygonal leptoma	小棒状,较长,顶端有不明显的微突起(plate Ⅲ:5) finely baculate, rather long, with nearly smooth processes on the top	Hebei, Mt. Wuling (河北,雾灵山) Du Gui-sen, W9546
丛生真藓 *B. caespiticium* L. ex Hedw.	(22.2~) 22.8 (~26.4)	具三角形薄壁区(plate Ⅱ:6) forming a triangular leptoma	小棒状,着生不规则,顶端有不明显的微突起(plate Ⅱ:5) finely baculate, arranged irregularly, with nearly smooth processes on the top	Xizang, Yadong (西藏,亚东) Xizang Exped, 7854
灰黄真藓 *B. pallens* Sw.	(10.5~) 11.3 (~13.6)	具近似菱形薄壁区(plate Ⅰ:8) forming a shuttle-shaped leptoma	棒状,着生规则,顶端有瘤状微突起(plate Ⅱ:4) baculate, arranged regularly, with gemmae on the top	Xizang, Milin (西藏,米林) Xizang Exped, 7494
拟三列真藓 *B. pseudotriquetrum* (Hedw.) Schwaegr.	(19.4~) 21.6 (~25.0)	具多角形薄壁区(plate Ⅱ:3) forming a polygonal leptoma	小棒状,着生相对较稀疏,且不均匀,顶端有颗粒状微突起(plate Ⅲ:2) finely baculate, arranged rather sparsely and unevenly, with granules on the top	Xizang, Chayu (西藏,察隅) Wang Mei-zhi, 12797-b
圆柱真藓 *B. paradoxum* Schwaegr.	(15.5~) 17.9 (~21.9)	具长圆三角形薄壁区(plate Ⅰ:7) forming a elliptic-triangular leptoma	短棒状,着生规则且较密,顶端有颗粒状微突起(plate Ⅱ:1) shortly baculate, arranged regularly and rather densely, with gemmae on the top	Yunnan, Gongshan (云南,贡山) Wang Mei-zhi, 9373-a
汤氏真藓 *B. thomsonii* Mitt.	(16.7~) 18.3 (~20.8)	具多角形薄壁区(plate Ⅲ:8) forming a polygonal leptoma	棒状,着生较密,顶端有不明显的微突起(plate Ⅱ:7) baculate, arranged rather densely, with nearly smooth processes on the top	Xizang, Linzhi (西藏,林芝) Lang Kai-yong, 675

表 1 (Cont.)

种 Species	孢子直径 Spore diameter(μm)	萌发孔 (SEM) Aperture	外壁纹饰 (SEM) Exine ornamentation	凭证标本 Voucher
蕊形真藓 *B. coronatum* Schwaegr.	(8.3～) 10.2 (～11.1)	具多角形薄壁区 (plate Ⅰ:3) forming a polygonal leptoma	短棒状，着生规则，相对较稀疏，顶端膨大成半球形 (plate Ⅱ:2) shortly baculate, arranged regularly and rather sparsely, the top of baculate expanded into hemispheroid	Yunnan, Menghai (云南，猛海) Luo Jian-xin, 86370
沙氏真藓 *B. sauteri* B.S.G.	(15.3～) 18.0 (～20.0)	具三角形薄壁区 (plate Ⅰ:5) forming a triangular leptoma	棒状，顶端膨大成半球形，有不明显的微突起 (plate Ⅱ:9) baculate, the top of baculate expanded into hemispheroid, with mearly smooth processes	Sichuan, Maerkang (四川，马尔康) He Si, 31279

Ⅲ. 棒状突起顶端膨大呈半球形。其种类有：*B. coronatum*；*B. sauteri*。

3.2　按孢子直径划分类群

Ⅰ. 孢子直径在 10 μm 以下的有 *B. uliginosum*。

Ⅱ. 孢子直径在 10～20 μm 之间的有：*B. argenteum*；*B. alpinum*；*B. coronatum*；*B. pallens*；*B. paradoxum*；*B. sauteri*；*B. thomsoii*。

Ⅲ. 孢子直径在 20～30 μm 之间的有：*B. pallescens*；*B. caespiticium*；*B. pseudotriquetrum*；*B. lonchocaulon*；*B. arcticum*。

由于 13 个种的孢子均具近极薄壁区(proximal leptoma)的萌发孔，外壁纹饰均为棒状，故真藓属确是一个自然分类群。其纹饰类型与孢子直径类群之间尚无明显的相关性，证明该属的分类交叉性状明显。

按真藓属孢子外壁纹饰归类，与关根雄次讨论的分组情况相比较，纹饰类型Ⅰ中包括了 Ochi (1959)等所划分的真藓属 Sect. Ptychostomum 中的 2 个种(*B. uliginosum*；*B. arcticum*)和 Sect. Eubryum 中的 3 个种(*B. argenteum*；*B. lonchocaulon*；*B. coronatum*)。纹饰类型Ⅱ中包括了 Sect. Leucodontium 中的 2 个种(*B. alpinum*；*B. pallens*)和 Sect. Eubryum 中的 4 个种(*B. pseudotriquetrum*；*B. caespiticium*；*B. paradoxum*；*B. pallescens*)。由此可见，真藓属植物的配子体、孢子体及孢子在形态结构上存在明显差异，种间的亲缘关系以及分亚属或组的问题，还需进一步探讨。

根据 Shaw (1981)对真藓科 Bryaceae 中丝瓜藓属 *Pohlia* Hedw. 的报道，*Pohlia* 孢子的外壁与 *Bryum* 孢子的外壁均具棒状突起。显而易见，两属有较大的相似性。然而 *Pohlia* 孢子外壁的棒状突起顶端多具有不规则的粗瘤，与 *Bryum* 孢子相比，*Bryum* 孢子外壁棒状突起顶端多具规则的半球形、刺状或疣状突起等，同时亦存在与 *Pohlia* 相同的纹饰类型。可以认为，*Bryum* 属的种类中存在原始与进化的不同类型，其多数种类较 *Pohlia* 属进化。根据我们近年来的工作，Bryaceae 孢子外壁的棒状突起较规则。比丛藓科 Pottiaceae 中孢子外壁不规则的刺状与瘤状突起(杜桂森等，1977)更为进化。

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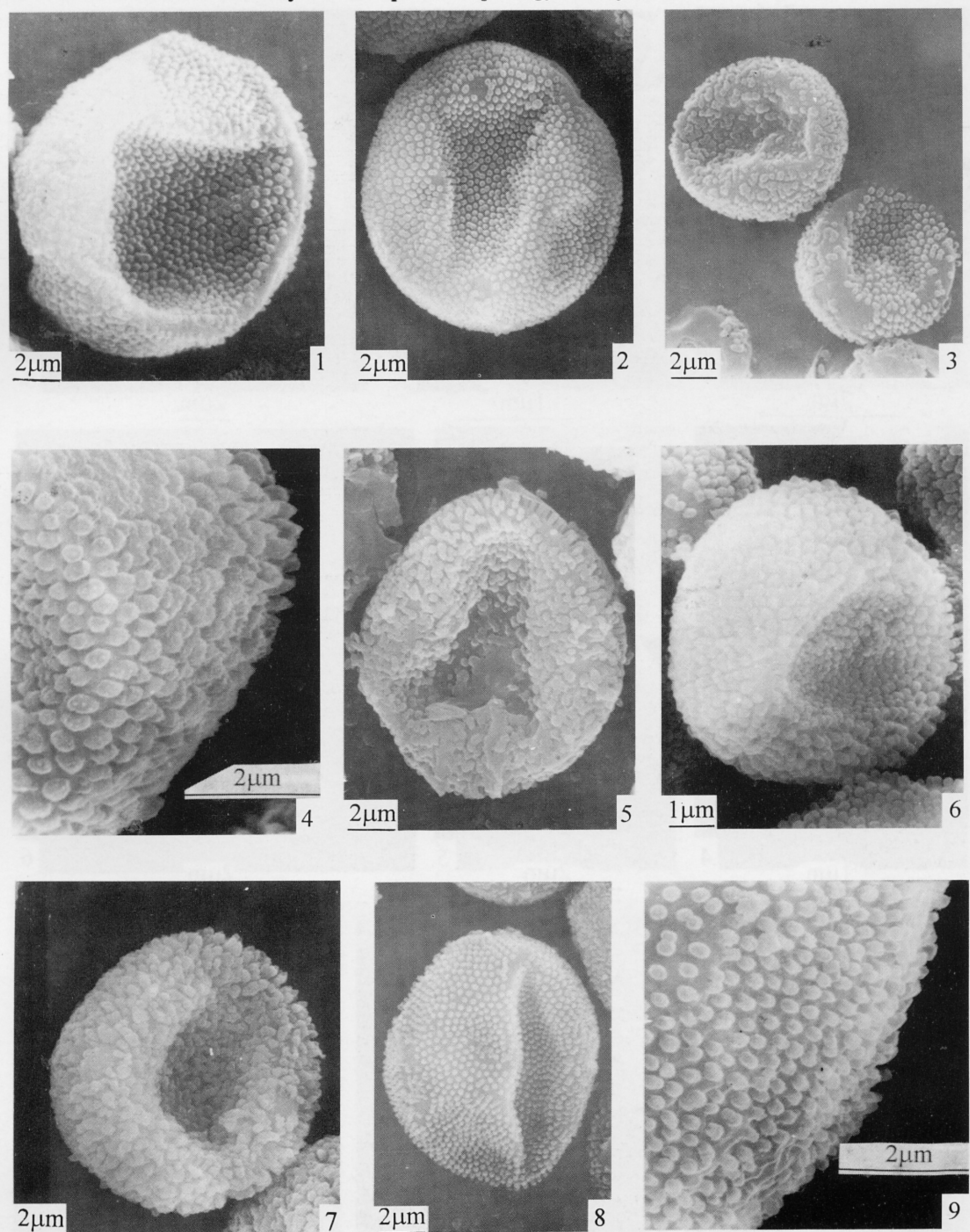
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图版说明 Explanation of plates

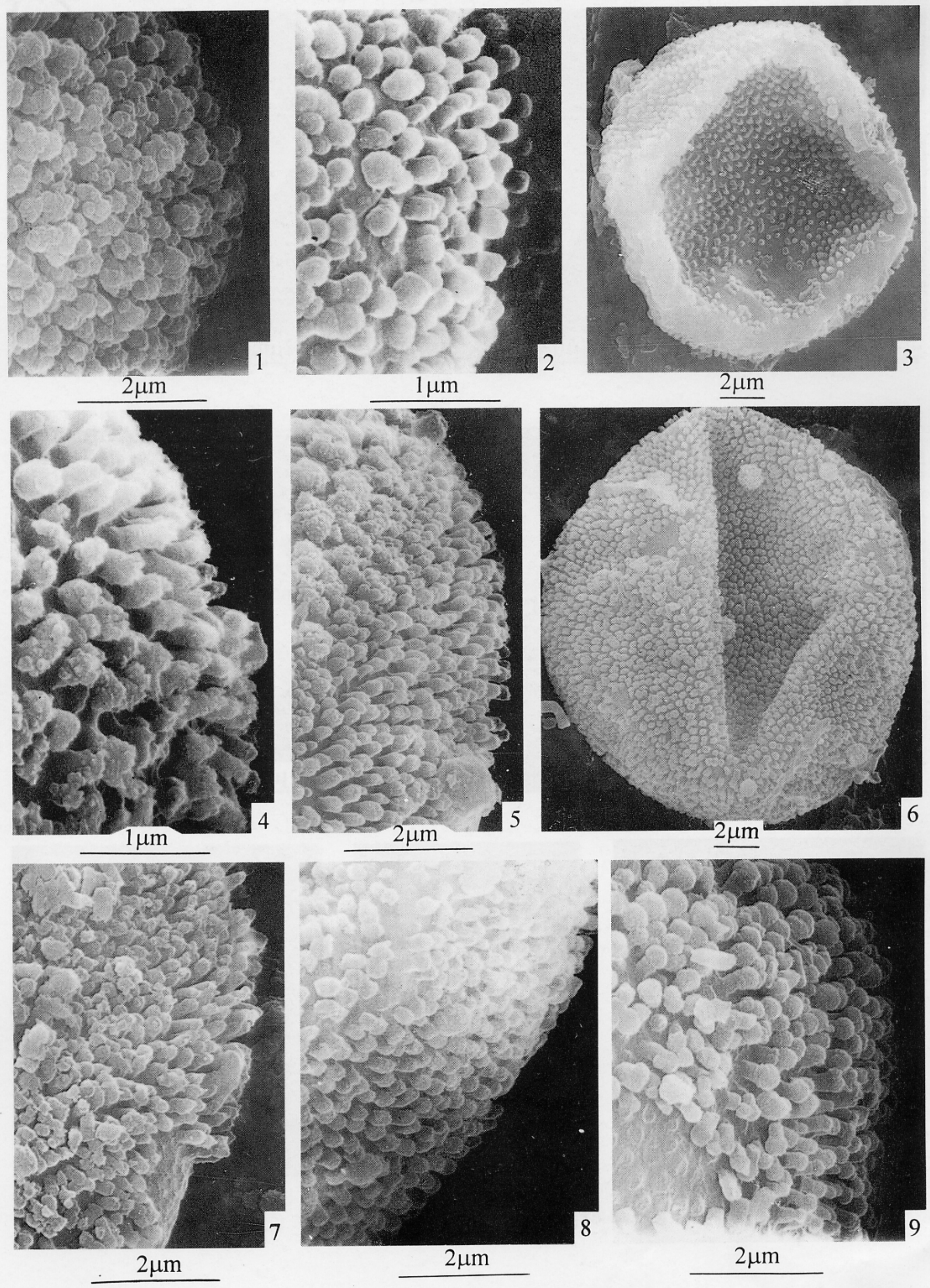
Plate Ⅰ 1. Proximal leptoma of *Bryum argenteum*; 2. Proximal leptoma of *B. pallescens*; 3. Proximal leptoma of *B. coronatum*; 4. Exine ornamentation of *B. pallescens*; 5. Proximal leptoma of *B. sauteri*; 6. Proximal leptoma of *B. uliginosum*; 7. Proximal leptoma of *B. paradoxum*; 8. Proximal leptoma of *B. pallens*; 9. Exine ornamentation of *B. lonchocaulon*.

Plate Ⅱ 1. Exine ornamentation of *B. paradoxum*; 2. Exine ornamentation of *B. coronatum*; 3. Proximal leptoma of *B. pseudotriquetrum*; 4. Exine ornamentation of *B. pallens*; 5. Exne ornamentation of *B. caespiticium*; 6. Proximal leptoma of *B. caespiticium*; 7. Exine ornamentation of *B. thomsonii*; 8. Exine ornamentation of *B. arcticum*; 9. Exine ornamentation of *B. sauteri*.

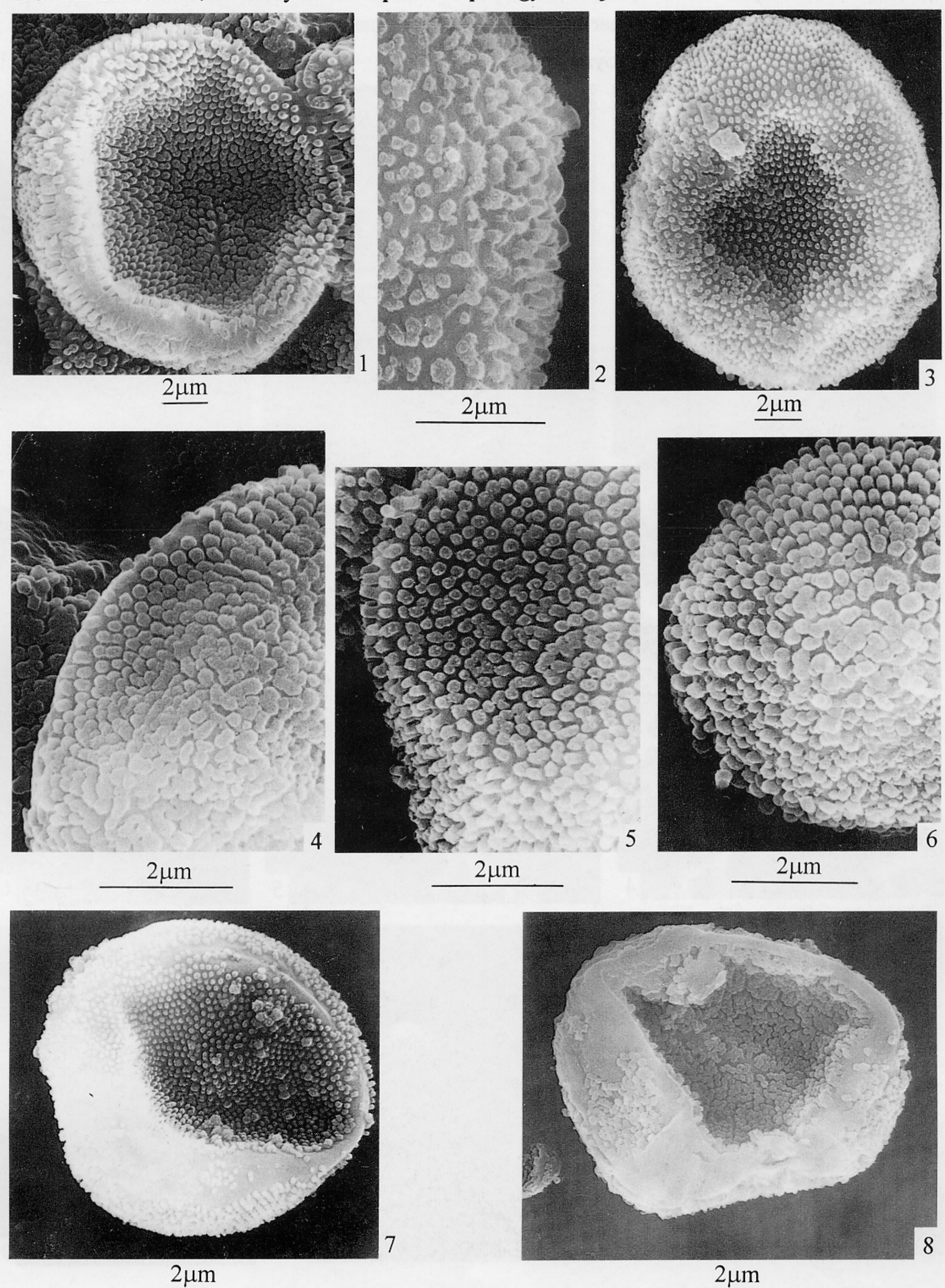
Plate Ⅲ 1. Proximal leptoma of *B. alpinum*; 2. Exine ornamentation of *B. pseudotriquetrum*; 3. Proximal leptoma of *B. arcticum*; 4. Exine ornamentation of *B. argenteum*; 5. Exine ornamentation of *B. alpinum*; 6. Exine ornamentation of *B. uliginosum*; 7. Proximal leptoma of *B. lonchocaulon*; 8. Proximal leptoma of *B. thomsonii*.



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